

COMPARATIVE EXTERNAL MORPHOLOGY OF 3 BOPYRID
 MALES (ISOPODA; EPICARIDEA) PARASITIC ON
CALLIANASSA UNCINATA H. MILNE EDWARDS

MORFOLOGIA EXTERNA COMPARADA DE 3 MACHOS BOPYRIDOS
 (ISOPODA: EPICARIDEA) PARASITOS DE *CALLIANASSA UNCINATA* H.
 MILNE EDWARDS

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ABSTRACT

The finding and description of the unknown male of *Ione ovata* Shiino, 1964, has allowed a detailed morphological comparison with the males of *Ionella agassizi* and *Pseudione brattstroemi*, all parasites of the ghost-shrimp *Callianassa uncinata* H. Milne Edwards in central Chile. Using scanning electron microscopy different types of setae—many apparently species-specific—are described from the antennae (1 and 2), the pereopods and the cephalon of each of these species. Position and structure of the buccal cone, buccal "palps", "slits" of the cephalon and other external characteristics are also described. Finally, the possible transcendence of these and other known adaptive features and general trends, for the taxonomy and phylogeny of the family is also discussed.

KEYWORDS: Males, bopyrids, morphology, Chile.

RESUMEN

Se compara la morfología externa de los machos de *Ionella agassizi* y *Pseudione brattstroemi* con el de *Ione ovata*, descrito aquí por primera vez, todos parásitos del "nape" *Callianassa uncinata* H. Milne Edwards, en Chile central. Su estudio con microscopía electrónica de barrido ha permitido describir e ilustrar varios tipos de setas observados en las anténulas y antenas, los pereópodos y el cefalón, muchos aparentemente especie-específicos. Se describe, también, y compara la posición y estructura del cono bucal, la presencia de "palpos" bucales, de las denominadas "hendiduras" del cefalón y otras características externas. Finalmente, se discute la posible transcendencia de estas y otras características adaptativas de los machos en la clasificación y filogenia del grupo.

INTRODUCTION

An interpretation of the phylogeny of bopyrid genera, as pointed out by Shiino (1965), cannot successfully be based on female characters alone because of their adaptation to the structure and function of the host branchial cavity. Males on the contrary, he believed, follow an orthogenetic course, not keeping pace with the changes occurring in the female. He, accordingly, suggested that male characters should also be taken into account in the phylogenetical analysis and concluded that evolution in the males tends to degeneration of pleopods and fusion of the somites, as in the females, but in a less extreme way.

Shiino proposed the differentiation of six groups, all directly or indirectly derived from a *Pseudione* type by increased fusion of the pleonites correlated with change to other crustaceans hosts. Unfortunately, bopyrean males show a complexity of many undescribed and unsatisfactory described features whose study should be undertaken in detail, before the interrelationships of the main types identified with groups of different genera can be clarified. As shown by Jones (1974) and Stuardo *et al.* (1986), structural details of the antennules, antennae, pereopods, setation and other external features disclosed in SEM studies, allow a better characterization of different species and pose interesting questions on their functional role and possible phylogenetic value.

The presence of three different species belonging to the genera *Pseudione*, *Ionella* and

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Ione, all found parasitizing the host *Callianassa uncinata* H. Milne Edwards in central Chile, has permitted the description of the unknown male for one of these species and the comparison of several of its external features, with those of the other two males parasites.

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MATERIAL AND METHODS

Host specimens were collected at Coliumo Bay, central Chile (36°32'S; 72°56'W) and are kept at the collections of the Museo de Zoología, Universidad de Concepción, Chile. Details of collection are given under material studied and measurements for each specimen presented in Table 1.

SEM treatment largely followed the techniques recommended by Jones and Fordy (1971) and Nielsen and Strømberg (1973a). Samples were examined using an Autoscan U-1 Siemen ETEC and photographed on Kodak Plus- X, 21 DIN film.

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LIST OF ABBREVIATIONS USED IN FIGURES AND TABLES

ant 1	= antennae 1 (antennules)
ant 2	= antennae 2
bc	= buccal cone (mouth)
c	= carpus
ce	= cephalon
d	= dactylus
de	= denticles
lsc	= lamellated scale
m	= merus
p	= propodus
pa	= palp
pe	= pereopod
pl	= pleopod
pm	= palm
pp	= papillose pad
sc	= scale
sl	= slit

sp	= sensory spine
T ₁	= types of setae
u	= uropod

DESCRIPTIONS

Ione ovata Shiino, 1964

Material examined

1. Two specimens. Dichato, central Chile. Lower intertidal, shallow water; sand. October 4, 1984, MZUC 10869. On females taken from *Callianassa uncinata*. One specimen treated for SEM.
2. Two specimens. Dichato, central Chile. Lower intertidal, shallow water; sand. October 18, 1984. MZUC 10870. On females taken from *C. uncinata*. One specimen prepared for transmission electron microscopy.

Male (First description). (Figs. 1a, b; 5-12).

Body slender, about one third as broad as long. Body regions clearly differentiated. Pleonal segments fused; pereonal segments greatly disjoined, separated by deep and broad lateral incisions (Fig. 1a, b). Whitish semitransparent in life, without pigments; yellowish opaque in alcohol.

Cephalon broadly triangular. Pigmented slits resembling eyes always discernible, transversally placed on the anterior half (Figs. 5, 6).

Buccal cone placed between the antennae; posteriorly accompanied by 2, closely set 3-segmented palp-like appendages, each ending with 2 long setae one thinner than the other (Fig. 6).

Antenna 1 (antennule) of 3 non scaly segments, the last one very different in size to the other two. Terminal segment dorsally displaced, with about 14 long smooth setae. Second segment cylindrical with a distally placed frontal area occupied by 13 distinct short setae; there are 2 additional thinner setae distally located on the dorsal border. Basal segment short, thick bearing 2 short brush-like setae (Figs. 6, 9).

Antenna 2 of 6 smooth, cylindrical segments, progressively narrowing towards the tip; second and fourth the longest. Second

Table 1
SPECIMENS STUDIED. MEASUREMENTS IN MM. (*TYPE SERIES)

Species	Maximal Length	Head Length	Head Width	Pereon Width (maximal)	Abdomen Length (maximal)	Abdomen Width (maximal)
<i>Pseudione brattstroemi</i> *						
1	4.50	0.30	0.90	1.00	1.70	1.10
2	3.00	0.30	0.70	0.90	1.25	0.95
3	4.90	0.40	1.00	1.60	2.10	1.70
4	4.40	0.20	1.05	1.45	1.80	1.65
5	5.50	0.45	1.00	1.50	2.10	1.75
6	6.00	0.65	1.20	1.65	2.40	1.85
7	4.90	0.45	1.05	1.50	2.00	1.60
8	6.50	0.50	1.30	2.00	2.40	2.00
9	4.80	0.50	1.05	1.65	2.00	1.70
10	5.30	0.40	1.05	1.60	1.90	1.70
11	4.80	0.50	1.15	1.50	1.90	1.70
<i>Ione ovata</i>						
1	6.00	1.10	1.25	2.05	2.30	3.10
2	6.50	0.50	1.10	1.90	2.20	3.10
3	8.00	0.65	1.25	2.00	2.50	3.20
4	5.37	0.50	1.37	2.12	2.12	3.00
<i>Ionella agassizii</i>						
1	6.00	0.70	1.30	1.60	1.20	1.60
2	5.50	0.50	1.30	2.00	1.30	1.90
3	7.12	0.68	1.50	2.37	2.12	2.25
4	7.75	0.75	1.62	2.62	1.75	2.50
5	7.12	0.62	1.50	2.56	2.00	2.50
6	6.50	0.62	1.44	2.37	1.75	2.25
7	7.87	0.75	1.62	2.62	2.00	2.37
8	6.50	0.62	1.37	2.25	1.62	2.25
9	6.75	0.75	1.50	2.37	1.87	2.12
10	6.50	0.62	1.37	2.25	1.50	2.00

segment with one short distal seta on the frontal border. Third segment with a group of 5 distal setae placed on a frontally projecting area. Fourth segment with a set of 10 similarly placed, medium sized setae. Fifth segment with a crown of about 20 long distal setae surrounding the base of the last segment. Sixth segment with about 8 terminal setae of the same length (Fig. 10).

Pereon with deeply separated (pinnatisclus), kidney-shaped pereomeres, the fourth and fifth wider. Margins of the first 2 pereomeres projecting backwards. No *medio-ventral* tubercles present.

Pereopods unequal in size, the last 2 larger. Dactylus well developed on all pereopods. Distal area of the carpus covered with composed,

concentrically lamellated scales and medium-sized setae. Palmar surface of the propodus covered with rows of similar scales and small setae (Figs. 11, 12).

Pleon with 5 fused but laterally differentiated pleomeres bearing each a lateral, elongated finger-like process as long as the width of the first pleonal segment (Fig. 8). No pleopods present. Pleotelson fused to the last pleomere having similar processes.

Pseudione brattstroemi Stuardo, Vega and Céspedes, 1986

Material Examined

1. One specimen. Station "11". Coliumo Bay, central Chile. Grab, 11.5 m; sand. August

- 25, 1983. Paratype MZUC 8045. On female taken from *Callianassa uncinata*. Treated for SEM.
2. One specimen; juvenile. Station "10". Coliumo Bay, central Chile. Grab, 10 m; sand. August 25, 1983. Paratype MZUC 8046. On female take from *C. uncinata*.
 3. Five specimens. Dichato, central Chile. Low intertidal, shallow water; sand. October 4, 1984. Allotype MZUC 8052 and paratypes MZUC 8048, 8049, and 8053. On female taken from *C. uncinata*.
 4. Two specimens. Dichato, central Chile. Lower intertidal, shallow water; sand. October 18, 1984. Paratypes MZUC 8054 and 8055. On females taken from *C. uncinata*. N° 8054 treated for SEM.
 5. Two specimens. Dichato, central Chile. Fishing gear, 4 m; sand. October 24, 1984. Paratype MZUC 8056 (Smithsonian Institution, Washington) and MZUC 8057 (Zoological Museum, Copenhagen). On females taken from *C. uncinata*.

Male. (Figs. 3a, b; 13-15).

Body slender, almost one fifth as broad as long. Body regions clearly differentiated; segments separated by strong lateral incisions.

Cephalon roughly oval, broader than long. Pigmented slits resembling eyes, always discernible, obliquely placed on the anterior half (Fig. 13).

Buccal cone, placed behind the antennae; posteriorly accompanied by a pair of apparently 2-segmented, small palp-like appendages, widely separated, ending in a small simple seta (Fig. 14).

Antenna 1 (antennule) of 3 segments, each extremely different in size to the next. Terminal segment (flagellum) with a group of about 11 terminal setae and a lateral isolated one. Second segment massive, cylindrical, with a set of 8 distal setae: 4 simple and 4 (2 on each side) branched. Basal segment obliquely bent with strong scales on its anterior part and around the internal and ventral parts; 2 sub-distal setae and small thin setae appear intermingled with the scales (Fig. 14).

Antenna 2 of 5 segments: basal segment short but massive forming a ventral protuberance heavily covered with projecting scales and thin setae; second segment the longest, laterally compressed, with one long distal seta, many scales and intermingled small thin setae along its ventral border; third segment short with only one long distal seta; fourth segment almost twice as long as the third with a constriction around the first 1/3 of its total length indicated by groups of setae; a triangular area with a group of 9 long setae is distally placed while other isolated setae surrounds the base of the terminal segment; fifth segment narrower than the preceding one, cylindrical, almost as long as the third segment, with a ring of subterminal long isolated setae and a bunch of about 13 terminal ones, 2 of them appearing extremely long (Fig. 14).

Pereon with segments roughly rectangular, narrow, of similar breadth, separated by deeply incised (*pinnatiscisus*) margins. No medio ventral tubercles present. Pereopods of nearly same size but with segments proportionally different. Pereopods 1-3 similar, (Fig. 15) with well developed dactylus and short merus and carpus. Posterior margins of the ischium, merus and carpus with small projecting scales and thin short setae, sparsely distributed. Carpus bearing a flat distal area with projecting fringed scales and groups of simple setae. Palmar surface of the propodus expanded with a row of 5 stout cuspidate-like setae and a proximal process also with fringed scales. Pereopods 4-7 with small rudimentary dactylus and very elongated carpus; posterior margins of ischium, merus, carpus and anterior border of base segment, scaly.

Pleon of six well developed pleomeres; first three or four larger than the pereomeres, becoming progressively smaller towards the end. Uropods similar in shape to the remaining pleomeres but smaller; no medio-ventral tubercles or pleopods present.

Ionella agassizi Bonnier, 1900

Material Examined

1. One specimen. Dichato, central Chile. Lower intertidal, shallow water; sand. October

- 4, 1984. MZUC 10871. On females taken from *Callianassa uncinata*. Treated for SEM.
2. One specimen. Dichato, central Chile. Lower intertidal, shallow water; sand. October 4, 1984. MZUC 10872. On female taken from *C. uncinata*. Prepared for transmission electron microscopy.
3. Eight specimens. Coliumo Bay, central Chile. August, 1982. MZUC 3139 (F. 1198). On females taken from *C. uncinata*.

Male (redescription): (Figs. 2a, b; 15-24)

Body thick somewhat short, less than 1/3 as broad as long. Pereonal segments not fused; first ones roughly rectangular, separated by deep incisions; 6-7 directed backwards. First pleonal segments not sharply differentiated from pereonal ones (Figs. 2a, b). Whitish semi-transparent in life; yellowish opaque in alcohol or formalin.

Cephalon ovate to trapeziform; covered with thin sometimes paired setae all around the borders but particularly towards the frontal and lateral margins. With postero-lateral eyespots. No slits are present, but a different structure is observed in the corresponding position (Figs. 16, 19).

Buccal cone placed between both antennae, conspicuously setting them apart. Posteriorly accompanied by 2 small apparently 2-segmented, closely set, palp-like appendages with only 1 terminal seta. One more pair of setae is notorious near the line of fusion of the basal segment (Fig. 12).

Antenna 1 of 3 non-scaly segments, the last one very small in size compared to the other two. Last segment laterally displaced, bearing about 5 simple, terminal setae and 2 double setae projecting from a long sheath ending in a sharp spine-like border. Second segment cylindrical, short, with 7 distal setae: 2 ramified ones on each side and 3 simple ones with long sheath on the internal border. Basal segment not bulky, with 2 ramified setae and 2 simple setae with long sheath projecting from an inner distal elevation (Figs. 17, 18).

Antenna 2 of 6 non-scaly segments and a long terminal flagellum; segments 2, 4 and 5 longer. Basal article short. Second segment long, with 4 medium-sized distal setae. Third segment short, bearing 3 setae with long sheath and 4 simple ones. Fourth segment

long, constricted, with 5 terminal and 4 sub-terminal simple setae. Segment 5, long with a crown of 11-12 terminal and 2 subterminal setae. Segment 6 short with about 6 long setae. Flagellum with 8 terminal long setae and an intermediate annulation (Figs. 19, 20).

Pereon well differentiated anteriorly. Pereomeres roughly rectangular, massive, with margins evenly rounded, deeply incised (*pin-natisiscus*); no medio-ventral tubercles are present.

Pereopods well developed, growing larger posteriorly (Fig. 19). Non scaly. Dactylus of the first pairs somewhat longer than the remaining ones, but all well developed; smooth. Palmar area of the propodus with large scale-like projecting denticles, arranged in irregular rows along two rims which form a central channel covered with large sensory spines. A few smaller sensory spines and long setae appear irregularly distributed among the denticles or along the rows. Around the scale-like denticles grow short papillae, which toward the base of the palm and on the adjacent area of the carpus, cover the denticles forming papillose pad-like sensory structures surrounding the large sensory spines. A similar arrangement is found on the distal part of the inner border of the merus (Figs. 21-23).

Pleon of 6 well developed pleomeres directed backwards, subequal in length. First pleomere as large as the pereomeres; remaining ones becoming progressively narrower; width of the last pleomere about the half of the first one. Five pairs of biramous pleopoda follow the pereopods, with the internal ramus (endopodite) rod-like shaped, arising from the basal part of the exopodite. Pleotelson small, forming a round tubercle. Uropoda uniramous, rod-like, ventrally directed (Fig. 24).

COMPARATIVE REMARKS

The males available for study are included in two of the six groups of genera recognized by Shiino (1965). *Pseudione* and *Ionella* belong to the "*Pseudione* group" and *Ione* to the "*Cepon* group".

Undoubtedly, evolution in the Bopyridae has involved the degeneration or modification of some organs and the development of new

ones. Degeneration of the pleopods, fusion of somites, greater development or reduction of coxal plates, lateral plates and oostegites appear particularly notorious in the females. Males, on the contrary, at the time of Shiino's conclusions appeared more conservative showing conspicuous changes in the degeneration of pleopods and uropods and fusion of the pleonites.

One has to agree with Shiino that evolution of males follows its own independent course and different pace, but this can only be understood if detailed morphological and functional studies are carried out in all genera and ideally in many species. Yet, the study of Jones (1974) on the males of one species of *Hemiarthrus*, the more detailed descriptions of the antennae of several species initiated by Markham (1972, 1973) and those of Goudeau (1970) and Coyle and Mueller (1981) on the cryptoniscid males of species of other families and our own studies, as compared to former work, indicate a structural complexity in the antennae, other appendages and the body in general, of possible phylogenetic and/or taxonomic value.

It is regrettable that we have not, so far, found other bopyrids in coastal waters of central Chile and, obviously, with the representative of 3 genera only one of which is monotypic, we cannot test Shiino's comprehensive conclusions. However, we consider it valuable to discuss the great differences found mostly on the appendages, the oral cone and surrounding structures, possibly reflecting reproductive and functional adaptations to 3 very different females (see Shiino, 1964 and Stuardo *et al.*, 1986) and parasitic life.

We will discuss these morphological structures following the sequence traditionally observed in the descriptions.

General form and size

As shown in figures 1-3 and table 1, the 3 species present dorsally some differences in general form but not in size. Obviously the fused pleonal segments, lateral processes and strong separation of the pereonal segments easily differentiate *Ione ovata* from the other two; however, clear cut differences for all the species are mostly observed ventrally, few fea-

tures being alike between two species as discussed in the following paragraphs.

Cephalon and presence or absence of small setae

The general form of the cephalon is usually vaguely described as roughly oval or trapeziform, but its form alone is not a good feature to differentiate the 3 species. However, in *Ionella* the borders of the cephalon and pereomeres are provided with conspicuous small setae isolated or with 1 or 2 smaller companions, sparsely distributed, growing out of large pits. In the other two species the cephalon appears smooth, being slightly pitted in *Ione ovata* with occasional very small setae distributed only along the borders of the pleomeres.

Small setae on the cephalon were also reported for several other species by Bourdon *et al.* (1980), as discussed further on, but an interpretation of the role played by these and other types of setae awaits ultrastructural studies.

Position and features of the buccal cone

Differences in the position of the oral cone with respect to the antennae are very notorious in the 3 species. Close contact and greater development of the antennule in *Pseudione brattstroemi* has displaced the oral cone backwards so that its base (?) appears behind the level of these appendages (Fig. 14), while in *Ione ovata* and *Ionella agassizi* the base is inserted between the antennules, separating them (Fig. 6, 18, 19). Similar tendencies are observed in the adult females of the same species; thus, the first antennae are of large size in *Pseudione* and apparently obliterated in the female of *Ionella*, so that the oral cone appears to project dorsally. Seen from this perspective, the forward displacement of the oral cone does not appear only as an adaptation to the living habits of the male but as trend affecting the species. Clear homology, nonetheless, ends here as the mouth parts in the female are strongly modified as regards to those of the males.

There seems to be no detailed study of the mouthparts of different adult bopyrid species

either males or females. As shown in figures 6, 14 and 17, there are clear external differences among the 3 studied species but no dissection was attempted. *Ione ovata* presents the distal part of the labrum and the posterior lip heavily covered with fringed scales, while in *Ionella*, the same area is denuded. In *Pseudione brattstroemi* it appears also scaly.

Mandible (stylets) projecting out of the oral cone appear different for each species while external muscle bundles and apertures conforming the buccal mass and surrounding areas (now under histological study in one of these species) pose questions about how the oral cone and mouth parts are working and whether an hydraulic mechanism supported by specialized musculature is involved.

Buccal "palps"

Unique paired appendages placed behind the oral cone are present in the three studied male species. They are well developed, 3 segmented and closely set in *Ione ovata* (Fig. 6); less developed, apparently 2-segmented and widely separated in *P. brattstroemi* but partly fused in *Ionella* (Fig. 18). The last segment present two long setae in *I. ovata*; only one in *Pseudione brattstroemi* and *Ionella agassizi*.

Similar paired structures have been drawn formerly only for *Pleurocryptella fimbriata* by Markham (1973) who describes them as "maxillipeds" with 2 terminal setae. Given their position and the lack of precise comparative studies we doubt that they are maxillipeds. Until clear relationships with the buccal parts can be established we have called them simply "palps".

Pigmented spots and "slits"

Pigmented patches have traditionally been described as eyes in the males of many species of this family. Jones (*op. cit.*) using scanning electron microscopy described a pair of "slits" previously considered eyes, located on the anterior half of the cephalon of *Hemiarthrus abdominalis* and, recently, Bourdon *et al.* (1980) observed them on many other species of the family. These 2 types of structures are present in the Chilean species. *I. ovata* and *P. brattstroemi* do not show pigmented patches but

have elongated slits on the anterior half of the cephalon, obliquely oriented towards the middle line (Figs. 5, 7, 13). In the former species they are centrally directed backwards and directed forwards in *Pseudione*, as shown in figures 5 and 13. *Ionella agassizi* presents coloured patches in the posterior half of the cephalon, not differentiated under the SEM; no elongated slits are present in this species but in the same position appear paired structures formed by 2 outgrowths showing symmetric annulation (Fig. 15).

Ventral "pores" of the pleotelson

One of the new structures disclosed by Jones (1974) in his SEM study of the male of *Hemiarthrus abdominalis* corresponds to repeated paired opening or "pores" found on the ventral surface of the pleotelson. Their function is unknown at present, although this author suggested that they "seem more likely to be the vestigial pleopods than genital openings". No genital openings are likely to be present in the pleotelson and histological studies are indispensable to validate Jones's interpretation, but as shown in figure 8, we have observed somewhat similar ventral structures in the pleotelson of *Ione ovata*. Whether in the last case they are true openings or simple folds, could not be clearly ascertained even at great SEM magnification. We could not determine if *Pseudione brattstroemi* shows pores or not due to the partly collapsed pleomeres. *Ionella agassizi*, on the contrary, has pleopods and no structures resembling pores were observed.

Antennae

Antenna 1 in the 3 studied males is roughly similar in size, with 3 clearly separated segments. The basal segment is large, bulky and scaly in *P. brattstroemi* (Fig. 14), but smooth and not massive in the other two (Figs. 9, 17, 8). There are, however, considerable differences in the number, size and specialization of the setae for each species as summarized in Table 2.

Antenna 2 presents marked differences in the 3 species, being shorter in *P. brattstroemi* with only 5 segments, with 6 in *I. ovata* and 7 in *I. agassizi*, including a long flagellum (Figs. 10, 20). The number and types of setae is also very

Table 2
 MAIN MORPHOLOGICAL CHARACTERISTICS OF THE MALES OF
IONE OVATA, *PSEUDIONE BRATTSTROEMI* AND *IONELLA AGASSIZI*

	<i>Ione ovata</i>	<i>Pseudione brattstroemi</i>	<i>Ionella agassizi</i>
Body size	Slender: 1/3 as broad as long	Slender. 1/5 as broad as long	Broadly fusiform. About 1/4 as broad as long
Head - pereon	Separated	Separated	Separated
Pleon - pereon	Very differentiated	Clearly differentiated	Not so clearly differentiated
Cephalon	Broadly triangular to trapeziform. Smooth	Roughly oval. Smooth	Trapeziform. Borders finely setose
Mouth (buccal cone)	Between 1st. antennae. With long palps	Behind 1st. antennae. With palps	Between 1st. antennae. With small palps
Eyes	No eyes	No eyes	Pigmented spots
Slits	Well developed	Well developed	No slits. Other structures.
Antenna 1	3 segments	2 segments	3 segments
Segment 1 + setae	Not massive, short, not scaly; 2 lateral setae + 1 strap-like seta	Large, bulky, obliquely bent, scaly; small setae	Not massive, not scaly; 2 ramified setae + 2 with long spiniform base, on distal process
Segment 2 + setae	Cylindrical; 13 short setae on distal area	Massive, cylindrical; 8 distal setae (4 simple + 4 branched)	Cylindrical; 2 ramified setae on each side + 3 with long spiniform base, on internal border
Segment 3 + setae	Small; 14 long smooth setae	Small; 11 setae + 1 lateral isolated	Small; 2 double setae with long spiniform base + about 5 simple ones
Antenna 2	6 segments	5 segments	7 segments (6 + long flagellum)
Segment 1 + setae	Short, smooth; no setae	Short, partly scaly; small thin setae	Short
2 + setae	Long; 1 distal seta	Long; small thin setae	Long; 4 distal medium sized setae
3 + setae	Short; 5 distal setae on frontal area	Short; 1 long distal seta	Short; 7 distal setae
4 + setae	Long, slightly constricted; 10 distal setae	Long, constricted; 9 long setae on distal area	Long constricted; 5 terminal + 4 subterminal setae
5 + setae	Short; crown of 20 long distal setae	Small; ring of subterminal setae + 13 terminal ones, two of them very long	Long; ring of 11 distal + 3 subterminal setae
6 + setae	Small, ca. 8 terminal setae	—	Short; ca. 6 long setae
7	—	—	Flagellum (constricted ?); 8 terminal setae
Pereon			
Pereomeres	Kidney-shaped, deeply separated (pinnatiscisus), 4th and 5th wider	Roughly rectangular, narrow; margins slightly projecting backwards, pinnatiscisus, of similar breadth	Roughly rectangular, massive, with margins evenly rounded; separated, 6th and 7th directed backwards
Pereopods. Size	Last 2 larger; segments unequal	Equal in size; segments unequal	Last 2 larger; segments unequal
Dactylus	First ones longer, all well developed; partly scaly	First ones longer, becoming rudimentary backwards; partly scaly	First ones somewhat longer but all well developed; not scaly
Propodus + palma	Rim with rows of simple setae and composed concentrically lamellated scales	With scales and cuspidate-like setae	Denticles and sensory spines in rows along central channel and surrounding rims

Table 2 (Cont.)

	<i>Ione ovata</i>	<i>Pseudione brattstroemi</i>	<i>Ionella agassizi</i>
Carpus + area	Composed concentrically lamellated scales and setae	With scales and elongated setae	Sensory spines and papillose pads, the latter found also on the merus
Pleon	All pleomeres fused	5 pleomeres, deeply separated; pleotelson similar	5 pleomeres separated; pleotelson different
Lateral processes	Finger-like processes	No processes	No processes
Pleopods	No pleopods	No pleopods	Pleopods biramous, 5 pairs
Uropods	Absent	Absent	Small, rod-like

different for each species (Table 2) so that the simple numerical notation used by Markham (1972b, 1973) in his descriptions does not seem appropriate.

Pereopods

Very little attention has been given to these appendages in the literature in spite of the great differences shown in many species of the group. Exceptions are the works of Markham (op. cit.) and the interesting papers by Goudeau (1970) and Coyle and Mueller (1981) on the male cryptoniscus of other families.

In *P. brattstroemi* all pereopods are approximately of equal size while in *I. ovata* the last two pairs are considerably larger than the preceding ones (Fig. 12). The last pereopods in *I. agassizi* become also larger but increase in size is gradual from the first pair to the last (Figs. 19, 22). Such differences are not necessarily associated to size of the various segments. In *P. brattstroemi* the first dactylus is longer, partly scaly, becoming progressively rudimentary backwards (Fig. 16). In the other 2 species the dactylus of the first pereopods is also longer but all appear nonetheless well developed. In *I. ovata* it is also partly scaly while in *I. agassizi* it is smooth.

In general, the dactylus, propodus and carpus show always important functional adaptations, different for each species. In particular the palmar area of the propodus and that part here called distal area of the carpus, seem to develop conspicuous sensorial structures. Thus, the palmar area of the first pereopods in *P. brattstroemi* has developed scales and cuspidate-like setae not found on the other 2 species (Fig. 16). The same area in *I. ovata*

forms a rim with rows of simple setae and composed, concentrically lamellated scales (Figs. 11, 12). In *I. agassizi* there are denticles and sensory spines arranged in rows along the floor of a central furrow and surrounding rims (Figs. 21, 23). Undoubtedly such different arrangements correspond with the size and reflexed position of the dactylus against the palmar area. The distal area of the carpus apparently serves a similar sensorial function, having similar structures. In *P. brattstroemi* there are scales and elongated setae; *I. ovata* presents similar lamellated scales and setae as in the palmar area and *I. agassizi* shows sensory spines and papillose pads found on the merus.

Pleonal lateral processes, pleopods and uropods

I. ovata is different to the other two species in having 5 pleomeres fused (in fact a generic feature) and finger-like processes (Fig. 8). On the contrary, pleomeres in *P. brattstroemi* are deeply incised and separated, with a terminal tubercle in the pleotelson.

Conspicuously, *I. agassizi* has 5 pairs of biramous pleopods, while the other 2 species lack them.

Types of setae

Stuardo et al. (1986) have described several different types of setae in the male and female of *Pseudione brattstroemi*, remarking that they further show no common external characteristics with those described for other crustacean species. No ultrastructural studies have yet been undertaken to test functional interpretations.

A comparison of the types of setae found in the 3 males here studied does not help to endeavor generalizations. Although a pattern for given groups of setae is identifiable within every species, there are no such patterns shared between species. An attempt is made here to describe and figure them in drawings and photographs, as follows:

Ione ovata
(Fig. 4; types 1-5)

Setae, apparently with or without terminal pore and an adjoining knob or finger-like apex.

1. (Type 1) Long, strap-like setae growing out of large pits. Found laterally on the first and second segment of antennae 1 (46.7-62.5 μm) (Fig. 9).
2. Simple setae with pore and slightly conical (nodular) or ill-defined annular base. Three types may be differentiated:
 - a) (Type 2) Very small setae sparsely distributed on the propodus and carpus of the pereopods and the borders of the pereomeres (16.7-20 μm) (Figs. 11, 12).
 - b) (Type 3) Short, medium-sized and long setae, arranged along antennae 2 (12.5-67.5 μm) (Fig. 10).
 - c) (Type 4) Medium-sized setae of the carpus of all pereopods with knob or finger-like end (36.7-46.7 μm) (Fig. 12).
3. (Type 5) Simple medium-sized and long setae without visible pore but with prominent knob or verrucose apex. Found on the palps and distal parts of each segment of antenna 1 (25.0-55.0 μm) (Figs. 9, 9b).

Pseudione brattstroemi
(Fig. 4; types 6-9)

Setae with and without terminal pore and adjoining knob.

1. (Type 6; this is type 11 of Stuardo *et al.*) Very small simple setae, single or with 1 or 2 smaller companions, growing out of large pits. Without pores. Found on the lateral parts of the propodus of all pereopods and the basal segments of the antennae. Few ones appear scattered on the borders of the pereomeres (8.0-12.0 μm) (Figs. 14a, 15).
2. (Type 7; types 7 and 8 of Stuardo *et al.*).

Simple, medium sized or long setae with slightly conical base, terminal pore and with or without distal knob. Found on the basal, second and 3rd. segment of antennae 1 and antennae 2, and on the carpus of all pereopods (12.5-66.0 μm) (Fig. 15).

3. (Type 8; type 9 of Stuardo *et al.*). Setae with inflated hemispherical base (cuspidate-like) and terminal pore. Found only on the palmar area of the propodus of all pereopods (22.0 μm) (Figs. 15, 15a).
4. (Type 9; type 10 of Stuardo *et al.*). Flat bearded (tufted) setae. Found laterally and distally on the second segment of antenna 1 (46.0-51.0 μm).

Ionella agassizi
(Fig. 4; types 10-15)

Setae appearing blunt or verrucose at the apex with hollow shaft but without pore (or not observable).

1. Setae growing out of large pits. Two types are recognizable:
 - a) (Type 10) Simple small setae, single or with 1 or 2 smaller companions. Present on the borders and dorsal part of the cephalon, pereomeres and the palmar area of the propodus (10.7-37.5 μm) (Figs. 17, 22).
 - b) (Type 11) Plumose setae. Found on the second segment and basal segment of antenna 1 (26.7-38.3 μm) (Fig. 17).
2. Simple setae with slightly conical (nodular) or ill-defined annular base. Comprise two types:
 - a) (Type 12) Long large setae of the terminal segment of antenna 1 (44.2-53.6 μm) (Fig. 17).
 - b) (Type 13) All setae of antenna 2, with sizes becoming progressively longer from the base upwards (20.5-57.5 μm) (Fig. 20).
3. (Type 14) Setae with long spiniform basal segment. Found on the second and terminal segment of antenna 1 and the second segment of antenna 2 (46.1-60.9 μm) (Fig. 17).
4. (Type 15) Sensory spine with seta. Found on the palmar area of the propodus and also on the carpus and merus of all pereopods (36.9-45.0 μm) (Figs. 21-23).

It appears noteworthy that, in the 3 species,

no typical aesthetascs are recognizable among all these types, least of all in the terminal segment of antenna 1. In fact, only the peculiar strap-like setae in *Ione ovata*, the tufted setae in *Pseudione brattstroemi* and the plumose setae in *Ionella agassizi*, all found on the first two segment of antenna 1 growing out of typical or modified pits, look like possible aesthetascs.

DISCUSSION

The comparison of the differences shown by the 3 species studied touch on two important aspects: the phylogenetic importance given to some trends used in supra-generic differentiation (Shiino, 1965; Codreanu, 1967; Markham 1972a, 1973, 1974, 1977) and the overall conjectural adaptative significance of many morphological structures.

As discussed by Shiino (*op. cit.*) or evinced by former authors, several trends seem to have determined the evolution of this family:

- a) Radiation following a monophyletic origin from external parasites.
- b) Evolutionary adaptation to given groups of crustacean Decapoda.
- c) Change of location (niche) of the parasite on the host's body.
- d) Complex development al cycles.

a) Monophyletic origin

Radiation is well exemplified in the female body starting from a generalized, rather symmetrical form in the ancestral parasites, purportedly represented nowadays by genera such as *Pleurocryptella*, *Gyge*, *Ionella* and particularly by forms of *Pseudione*, and culminating in the strongly asymmetrical and modified forms of *Hemiarthrus*, the anteriorly modified *Athelges*, and others.

In contrast, the radiation of males was minimal, at least in the general form. Lost of pleopods and uropoda seem to have occurred early in the evolution of the family. Fusion of the pleonites, on the other hand, was not general although branching from the original ancestor often ended in partial or total fusion. Pertinently, fusion of pereonites also occurred and was described by Markham (1972a) for his *Hemiarthrinae* as discussed further below.

b) Adaptation to given groups of decapods

Radiation from ancestral species has been strongly directed by evolutionary adaptation to decapod's hosts. Thus, from apparently *Pseudione*-like ancestors, derived the 3 main phylogenetic branches living in the branchial chamber of the hosts. One of these, initially parasitizing Anomura (mainly Galatheidae) radiated invading other groups of Macrura (Thalassinidea), therefore, covering hosts with either demersal, benthic or infaunal habits. A second line, specialized in the Caridea (e.g., *Alpheus*, *Synalpheus*, *Pandalus*, *Spirotocaris*, *Thor*). A third branch involved fundamental changes in the evolution of the Bopyridae, giving rise to several phyletic lines. One, with conservative traits radiated as parasites of the branchial chamber of the Peneidae. Another line, with strong pleonal differentiation of the female, mostly became parasites of the branchial chamber of Brachyura (e.g. *Uca*, *Pachygrapsus*, *Pinnotheres*) although one particular genus parasitized the thalassinidean Callianassidae: the genus *Ione*.

c) Change of parasite's niche

At this point of radiation, a new niche was open to the members of this family and phylogeny proceeded along two new phyletic lines dwelling on the abdomen of benthic living decapods. According to Shiino (*op. cit.*) the new lines arose from *Phyllodorus*-like ancestors. One line including the single known species of *Phyllodorus* evolved parasitizing Thalassinidea and Paguridea with nearly symmetrical females attached to the dorsal part of its host's abdomen. The other returned to Caridean hosts, as ventral abdominal parasites of shrimps and prawns, with females hypertrophied in only one side.

As we have mentioned, no definite taxonomic status were assigned to these phyletic lines, being simply proposed as *Pseudione*-group, *Bopyrus*-group, *Orbione*-group, *Cepon*-group, *Athelges*-group and *Phryxus*-group.

In fact, at the time of Shiino's paper, few authors had attempted to correlate phylogenetic trends with subfamilial ranks. Only Codreanu and Codreanu (1956) and later R. Codreanu (1967), on the basis of

characters of the females proposed a total of 8 subfamilies adding the new monotypic Bopyrophryxinae, Entophilinae and Phyllothurinae to the former names. Later, however, Markham (1972a) although recognizing that the status of these groups is largely a matter of personal opinion, formally proposed the subfamily Hemiarthrinae (=Phryxinae Codreanu & Codreanu, 1956) and later (1977) the subfamily Argeiinae, giving in both cases very complete diagnosis for both male and female. Most interestingly, he described the males of *Loki circumsaltanus* Markham 1972 and *Dicropleon periclimenis* Markham, 1972 with the pereonites partly fused as a further simplification of male morphology and the latter species with the abdomen ending in a prominent anal tube, a feature so far recorded only for the male of *Hemiarthrus abdominalis* by Jones (1974) and the larval (epicaridium and some cryptoniscus) stages of the family.

One cannot avoid speculating if these morphological changes departing from the stereotyped male's features are secondary simplifications or represent the preservation of larval features (neoteny). Whatever the true answer, these and other features suggest that adaptation in males may indeed have determined different phyletic trends.

Thus, aside from the degeneration of pereopods and uropods, and the fusion of the pleonites suggested as definite phyletic trends in males, departing from the ancestral general form, some other tendencies can be postulated. Obviously, evolution of male features may include both adaptive changes and the permanency of conservative traits. Among the latter, body size, presence of buccal cone, 3-segmented antennules and fixed number of pereopods and pereomeres can be considered generalized traits with definite phylogenetic value.

A number of other features of definite adaptive value have been observed in some species and are listed in table 3. However, minimization of the male taxonomic value, emphasis on female description and only occasional use of SEM, has prevented their discovery and precise study. This is the case of the "slits" on the cephalon and ventral "pores" in the pleon, discovered by Jones (*op. cit.*), the

differentiation of sensory structures in all appendages (aesthetascs, different types of setae, scales, etc.), fusion of pereomeres and so on.

Slits and small types of setae began to be studied only recently. In effect, Bourdon *et al.* (1980) advanced preliminary evidence on the presence of slits (fentes céphaliques) and "microsetae" in 46 species of Bopyrina, including one species of *Ione* and 3 of *Pseudione*. They remarked that slits were found in the males of all the species studied as well as on other undescribed and unidentified ones; most interestingly, slits were also found on the females, although it was not clearly stated if all females had them.

Using histological sections they demonstrated that the slits represent true ducts running almost vertically through the cephalon, with ventral openings located between the basis of antennae and antennules or above them. They further concluded that their position, form and direction change from species to species. Thus, they can have an anterior, medial or posterior (eyes level) position, be narrow and elongated with borders resembling lateral lips and their main axis convergent or divergent to the medial line, or round, triangular and even curved in shape.

Our own study is largely consistent with some of these observations and we do not doubt that the slits present in the cephalon of *Ione ovata* and *Pseudione brattstroemi* are homologous to those found by Jones (*op. cit.*) and Bourdon *et al.* (*op. cit.*) for other species of Bopyrina. However, we have also demonstrated that it is not a generalized feature as no slits are present in the male of *Ionella agassizi* and they were not found on the females of these 3 species.

Very small setae called "microsetae" were also unmasked by Bourdon *et al.* (*op. cit.*) resembling similar setae described by former authors for some decapod crustaceans. They were figured symmetrically arranged in patterns apparently species specific and, accordingly, of possible systematic value. They were further characterized as either isolated, bifid or trifid setae growing out of pits bounded by annular thickenings of the cuticle. One additional type named medium-sized microsetae (microsètes médianes) was always found pre-

sent between the slits or behind them. Unfortunately, no reference was made to their presence on other parts of the body.

We must assume that either the so-called "microsetae" or the medium-sized ones might correspond to the small type found by us on the cephalon of *Ionella agassizi*; in fact, as shown in our figure 16, there seem to be a few pairs somewhat symmetrically arranged. However, as discussed above, they are definitely not present on the cephalon of the other 2 species although small setae appeared on other parts of the body or appendages.

Undoubtedly, only detailed descriptions of the males (and females) in many species, and in particular a combination of histological and functional studies will allow the evaluation of the possible use of all these structures in taxonomic differentiation and phylogenetic analysis.

d) Complex developmental cycles

Published evidence so far supports the conclusion that most bopyrids and Epicaridea in general, undergo larval development represented by typical epicaridium and cryptoniscus stages, with an intermediate metamorphosing microniscus stage, parasitic on copepods and post-cryptoniscus metamorphosing stages on the final host (see valuable literature reviews in Veillet, 1945; Reinhard, 1949; Strømberg, 1971; Nielsen and Strømberg, 1973b; Goudeau, 1967, 1970; Anderson and Dale, 1981; Beck 1980; Coyle and Mueller, 1981; Dale and Anderson, 1982). We may now add that plankton sampling carried out at Coliumo Bay in central Chile, confirms that this is also the case for the 3 species here studied. However, as Strømberg (1971) pointed out such generalizations do not mean that all "bopyrids" follow this developmental sequence. At least in another family the case of *Entoniscoides okadai* (Miyashita, 1940) is known with a cryptoniscus larva developing directly from the egg.

Likewise, larval stages and metamorphosis imply not only differences in larval structures and organs between 2 distinct stages but also differences as regard to adult (male and females) features. Nielsen and Strømberg (*op. cit.*) studying the larvae of *Cryptoniscina* pro-

posed the series of morphological features which are now used in the description of all larval stages. They are so different to adult features that practically a complementary taxonomy had to be initiated. These authors did not suggest phylogenetic trends as the whole classification of the Cryptoniscina had to be reshaped, but here as in the Bopyridae, conservative as well as advanced larval traits may be recognizable. But, can they be meaningfully arranged in phylogenetic larval trends? Strømberg (1971) studying the possibility that some larval trends could be interpreted from cleavage and segmentation concluded that "it is so far difficult and dangerous to draw phylogenetic conclusions from embryology". His inference is valid until larval morphology in many genera and species can be better known.

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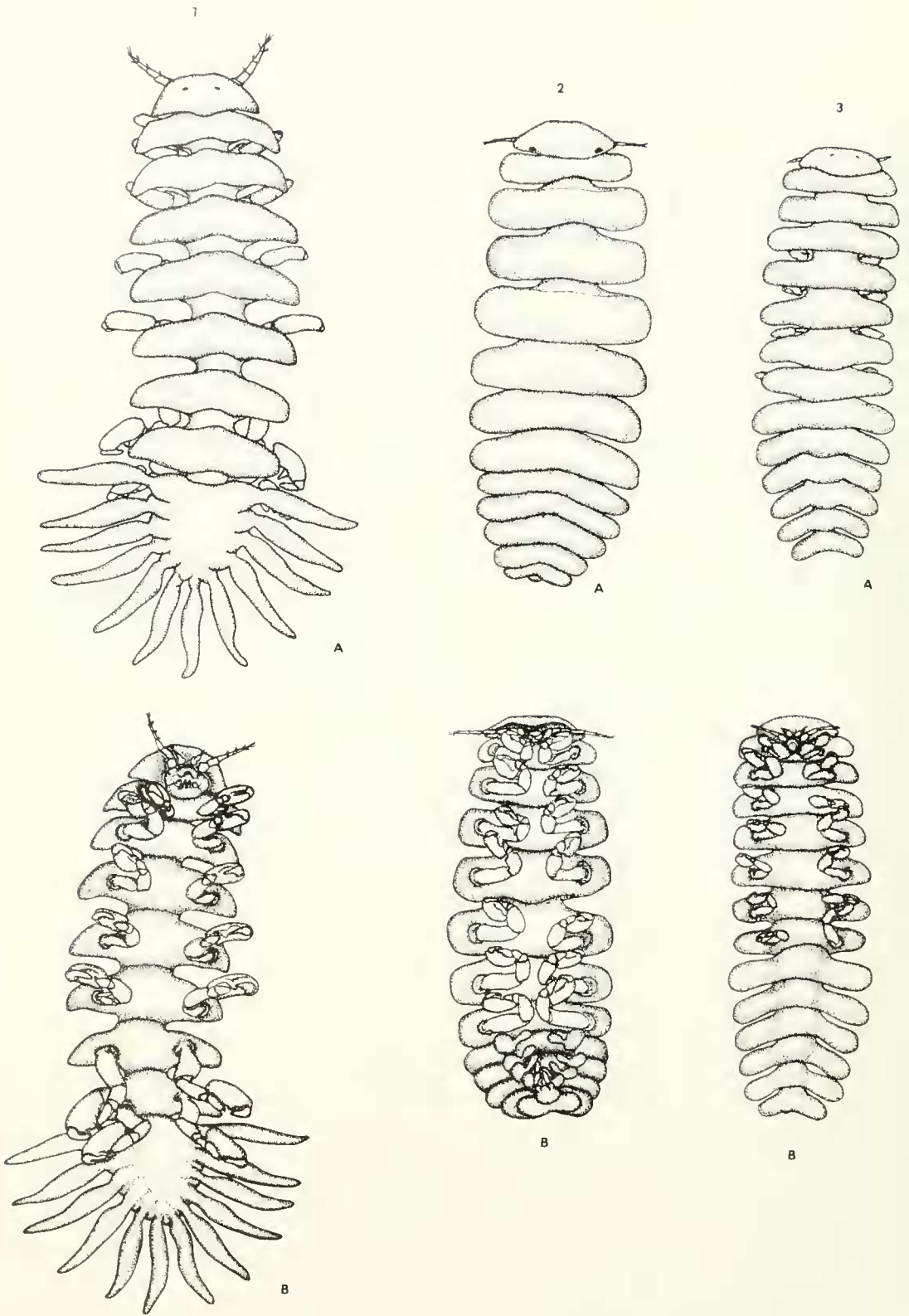
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Table 3
POSSIBLE ADAPTIVE TRENDS SHOWN AS CONSTANCY OR CHANGE
IN EXTERNAL MORPHOLOGY, AFFECTING MALES OF BOPYRIDAE

Body size	Fairly constant.
Fusion of cephalon-pereon	Rare; no definite trends (Markham, 1973).
Fusion of pereomeres	Rare; recorded in Hemiarthrinae (Markham, 1972).
Fusion of pereon-pleon	Not observed.
Fusion of pleomeres	Common. Tendency follows adaptive trend (Shiino, 1965).
Buccal cone	Apparently constant.
Position regarding orientation	Forward or backward, the latter more common.
Position regarding antennulae	Behind or between; this study.
"Palps"	Few records (Markham, 1973; this study).
Eyes (posterior)	With or without. No clear trends.
"Slits"	With or without. Few records (Jones, 1974; Bourdon <i>et al.</i> , 1980; this study).
Antenna 1 (antennule)	Well developed, 3-segmented. Adaptive constancy.
Aesthetascs	Not differentiated. Little studied.
Setae	Many types. Strongly differentiated. Few detailed observations (Bourdon <i>et al.</i> , 1980; this study).
Antenna 2	Well developed. Segments very variable.
Flagellum	No clear records.
Pereomeres	Constant in number. Variable in shape.
Pereopods	Constant in number. Variable in size and setation.
Ventral tubercles	Variable (Markham, 1973). Present or absent.
Pleomeres	Different in shape and size. Apparent trends regarding fusion or elongation.
Lateral processes	Variable in shape; not constant.
Pleopods	Present, modified or absent. Degeneration shown as adaptive trend (Shiino, 1965).
"Pores"	Few records (Jones, 1974, this study). Related to precedent trend?
Uropods	Present, modified or absent. Degeneration shown as adaptive trend (Shiino, 1965).
Anal tube	Only in Hemiarthrinae (Markham, 1972a; Jones, 1974).

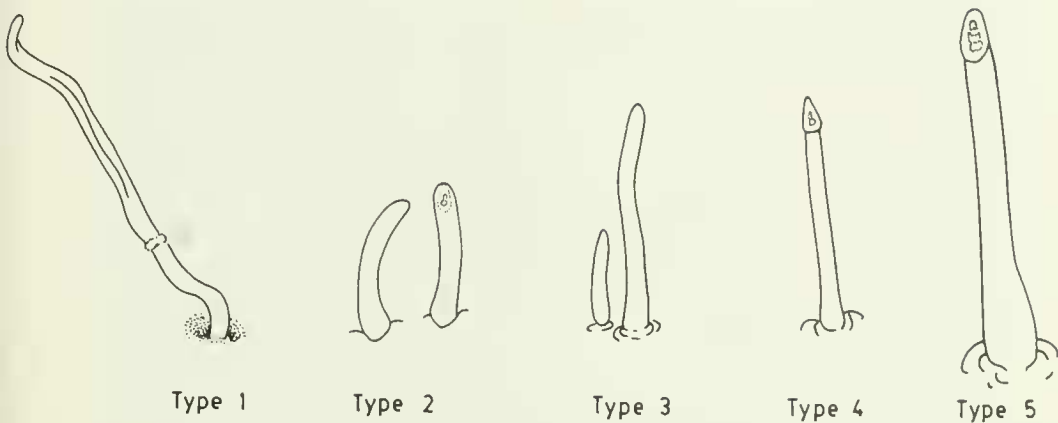
Table 4
COMPARATIVE DISTRIBUTION OF SETAL TYPES ON THE BODY AND
APPENDAGES OF *IONE OVATA*,
PSEUDIONE BRATTSTROEMI AND *IONELLA AGASSIZI*

	<i>Ione ovata</i>	<i>Pseudione brattstroemi</i>	<i>Ionella agassizi</i>
Cephalon			T ₁₀
Antenna 1			
segment 1	T ₁ T ₅	T ₆ T ₇	T ₁₁
segment 2	T ₁ T ₅	T ₇ T ₉	T ₁₁ T ₁₄
segment 3	T ₅	T ₇	T ₁₂ T ₁₄
Antenna 2	T ₃	T ₆ T ₇	T ₁₃ T ₁₄
Pereopod	T ₂		
propodus	T ₂	T ₆ T ₈	T ₁₀ T ₁₅
carpus	T ₂ T ₄	T ₇	T ₁₅
merus			T ₁₅
Pereomeres	T ₂	T ₆	T ₁₀
Palps	T ₅		

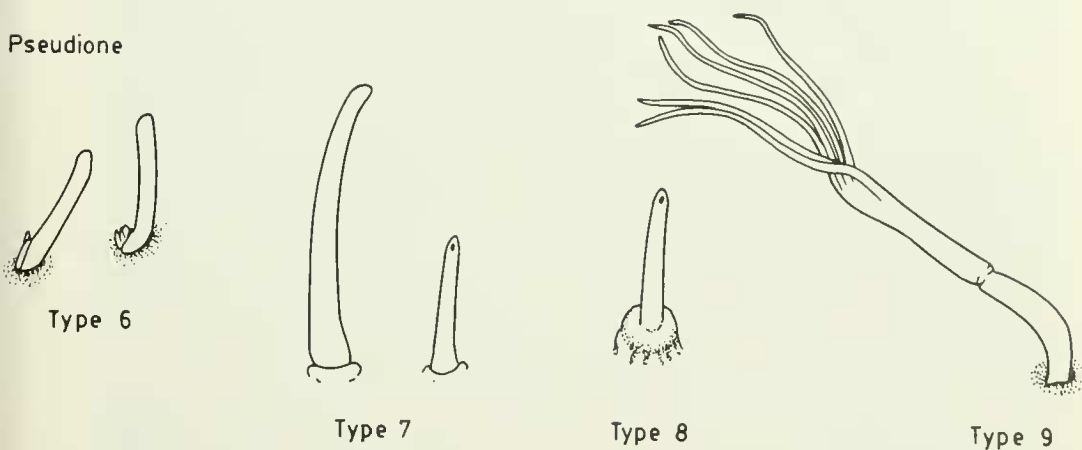


FIGS. 1-3. Dorsal and ventral view of the males of *Ione ovata* (1A, 1B) *Ionella agassizi* (2A, 2B) and *Pseudione brattstroemi* (3A, 3B) (compare measurements in Table 1).

Ione



Pseudione



Ionella

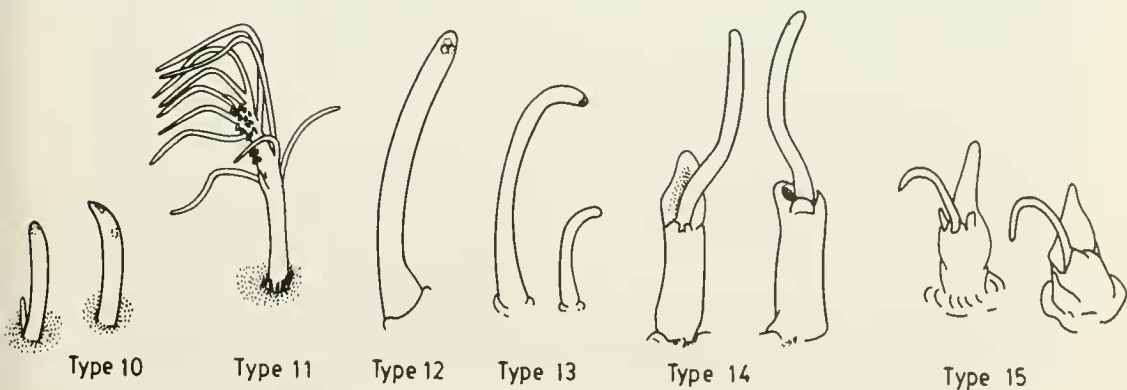
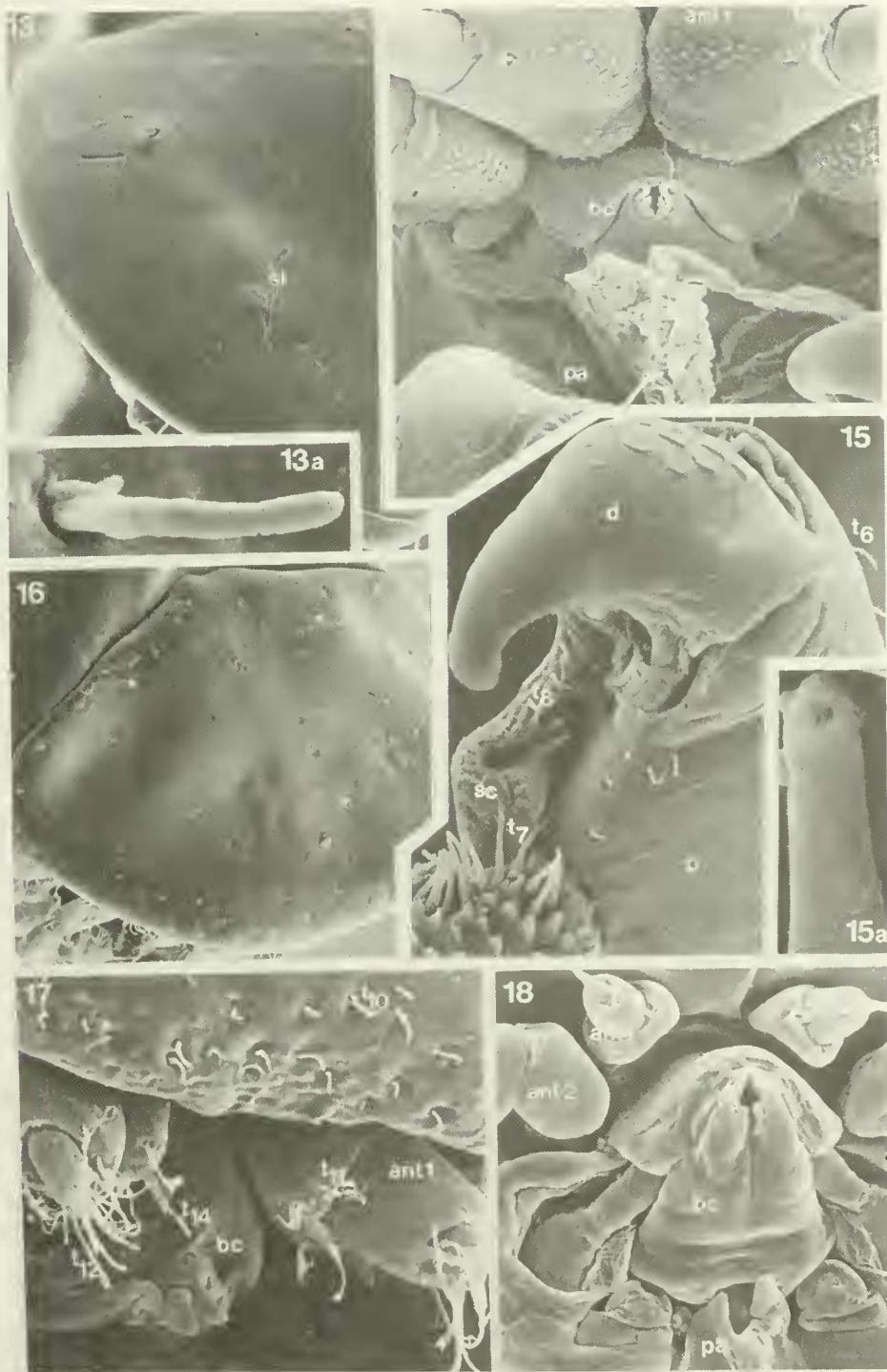


FIG. 4. Main types of setae found on the males of the 3 species studied. *Ione ovata*: types 1, 2, 3, 4 and 5. *Pseudione brattstroemi*: types 6, 7, 8 and 9. *Ionella agassizi*: types 10, 11, 12, 13, 14 and 15. (See text).

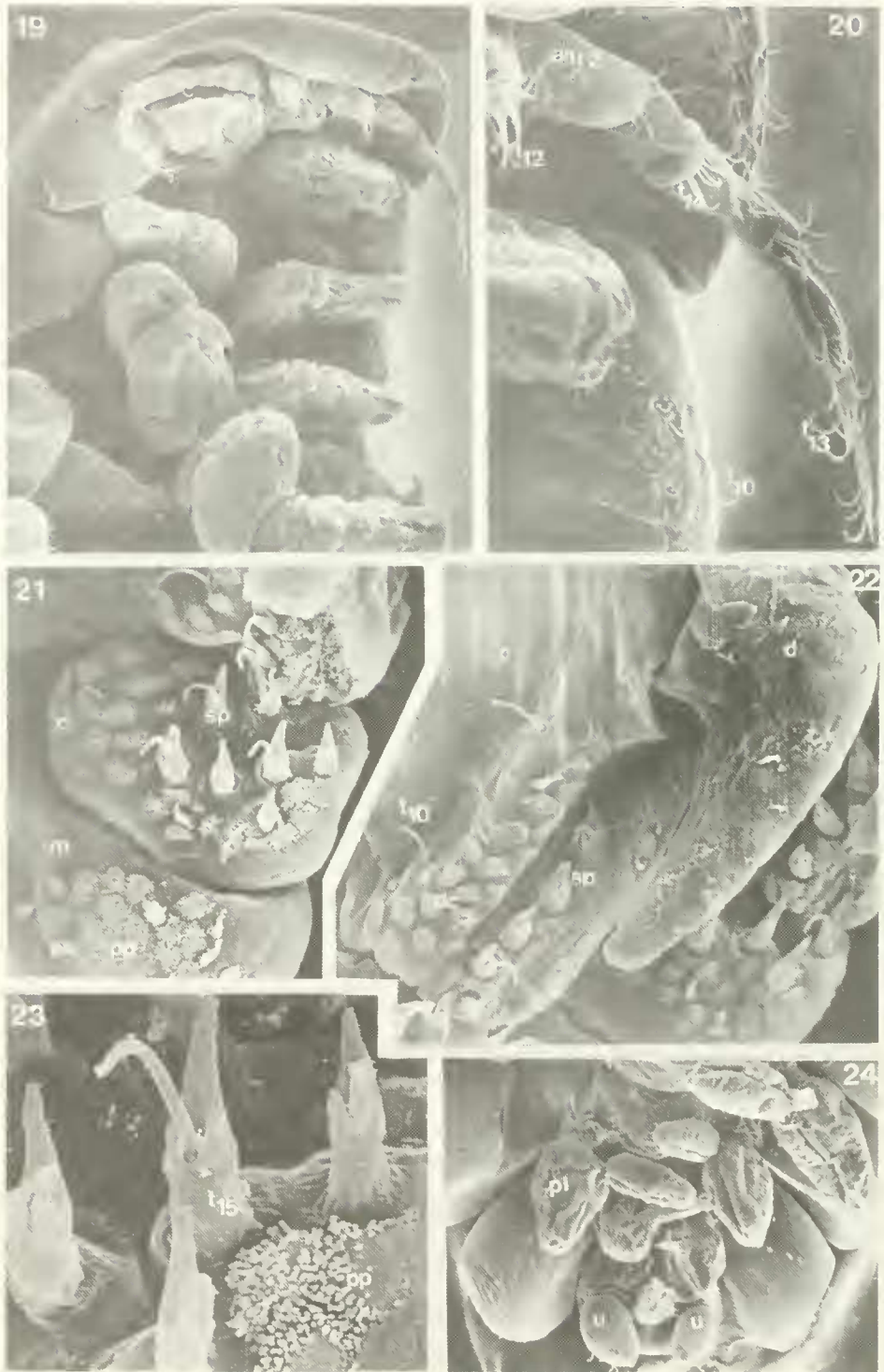


FIGS. 5 - 12. *Ione ovata*. Male. 5. Frontal view of the cephalon, first peromeres and surrounding appendages. Note the position and comparative size of the "slits" (x 40). 6. Buccal cone inserted between the antennules, showing protruding stylets and adjacent palps (x 150). 7. Enlarged view of a "slit" (x 800). 8. Ventral view of the partly collapsed pleonal processes (x 31). 9. Right antennule (antenna 1), showing setae of types 1 and 5 (x 400). a. Tip of type 5 (x 8500). 10. Terminal segments of antenna 2, showing setae of type 3 (x 400). 11. Concentrically lamellated scales and setae of the palm of pereopod 3 (x 1600). 12. Right pereopods of the second and third pair, showing scales and setae of types 2 and 4 (x 150).



FIGS. 13 - 15. *Pseudione brattstroemi*. Male. 13. Frontal view of the cephalon showing position of the slits (covered by bacterial growth) (x 80). a. Detail of small seta of type 6 (x 4000). 14. Buccal cone inserted behind the antennules, showing protruding stylets and labrum. The scaly areas of the basal segment of both pairs of antennae are particularly notorious (x 190). 15. Details of the distal area of the carpus, palm and dactylus of the left fourth pereopod showing scales and setal types 6, 7 and 8 (x 450). a. Tip of cuspidate-like seta (Type 8) (x 8000).

FIGS. 16-18. *Ionella agassizi*. Male. 16. Upper frontal view of the cephalon without "slits" (x 80). 17. Border of the cephalon, antennules and buccal cone seen in frontal view (x 280). 18. Ventral view showing details of the buccal cone, antennules, basal segments of antenna 2 and "palps" (x 115).



FIGS. 19-24. *Ionella agassizi*. Male. 19. Ventral view of the anterior half (x 56). 20. Ventral view of the cephalon, first pereopod and antennae showing setae of types 10, 12 and 13 (x 195). 21. Second pereopod. Distal areas of the merus and carpus showing sensory spines and papillose pad-like structures (x 480). 22. Left second pereopod. Propodus showing denticles, sensory spines and small setae of type 10 (x 440). 23. Ibid. Enlarged view of sensory spines and papillose pad. 24. Ventral view of the last pleomeres showing biramous pleopoda, pleotelson and rod-like uniramous uropoda (x 80).